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Sensory-Motor Plasticity of Virtual Body-Ownership

Submitted by Patrick Fasthén to the University of Skövde as a final year project towards the degree of Master of Science, MSc. in the School of Bioscience. The project has been supervised by Oskar MacGregor.

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I hereby certify that all material in this final year project which is not my own work has been identified and that no work is included for which a degree has already been conferred on me.

Signature: _____

Acknowledgment

"*If you open your mind too much, your brain will fall out*" – Tim Minchin

Abstract

The distinction between the sense of body-ownership and the sense of agency has attracted considerable empirical and theoretical interest lately. However, the respective contributions of multisensory and sensorimotor integration to these two varieties of body experience are still the subject of ongoing research. In this study, I examine the various methodological problems encountered in the empirical study of body-ownership and agency with the use of novel immersive virtual environment technology to investigate the interplay between sensory and motor information. More specifically, the focus is on testing the relative contributions and possible interactions of visual-tactile and visual-motor contingencies implemented under the same experimental protocol. The effect of this is supported by physiological measurements obtained from skin conductance responses and heart rate. The findings outline a relatively simple method for identifying the necessary and sufficient conditions for the experience of body-ownership and agency, as studied with immersive virtual environment technology.

Keywords: Body-ownership, multisensory integration, agency, sensorimotor integration, rubber hand illusion, voluntary action, virtual reality.

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Introduction

Since the development of the computer as a scientific tool, we have witnessed several proposals for novel ways of dealing with complexity (e.g., chaos theory, complex networks, etc.). Despite not always fulfilling their stated potential, I believe these ideas have helped us increase our understanding of system theory and generally left us with new concepts and ways of formulating questions. If there is a contemporary domain of inquiry where complexity is severely underestimated and where linear thinking is bound to fail, this is the realm of cognition. The emerging picture of the brain is by no means a simple one, as it reveals subtle complexities and integration of factors that are not always easy to isolate. There is a recognized need to supplement the scientific categories of mechanistic thinking for new ways of thinking about non-linear forms of interactions and inter-relations between processes at multiple levels.

Metzinger (1995) once characterized the unity of our subjective reality by pointing to the strong experience that I am *one* person in *one* world. This perpetual holistic model created by the brain is a good example of a stunningly complex system. Different kinds of sensory information travel from sources to receptors at different speeds (e.g., by light or sound), and take different amounts of time to process (e.g., color and shape). However, perception does not seem temporally disjoint. How is this possible? According to a prominent theory in complex neural systems known as *temporal binding*, perceptual systems "wait" for the slowest process to complete itself before being integrated into perceptual representations (Bechtel & Richardson, 1993).

This raises two important questions. Is there a temporal window over which sensory information is integrated? And if so, is any such temporal window of a fixed duration or more flexible in nature? Binding, or on a more philosophical note, the unity of consciousness, refers to the ability of the brain to produce coherent, integrated representations of the world, although information is received in multiple forms through numerous sensory channels. Binding and integration, thus conceived, take place at many different levels of description or organization. Early research on self-consciousness has focused on high-level descriptions such as language, conceptual knowledge, or memory. In this essay, I will highlight some more recent discoveries related to low-level contributions, such as the role of multisensory and sensorimotor integration.

Multisensory Integration

Attempts to understand the principles behind our perception of the world have for long been dominated by a focus on the individual senses. However, the past decade has witnessed a growing shift of emphasis away from the study of the senses in isolation, as systematic efforts have been taken to examine the interactions between different sensory modalities. This recognizable and multidisciplinary field is known as *multisensory integration*, and is the study of how information from different senses forms coherent and robust perceptual experiences. Surrounded by multiple sources of sensory stimulation, the brain is ultimately faced with the task of whether to integrate or segregate specific categories of temporally congruent sensory input based on the degree of spatial and structural congruence of those stimulations (Stein, 2012).

For example, when we hear a car alarm, we determine which car triggers the sound by which car we see is spatially closest to where we perceive the origin of the sound. In other words, the auditory and visual information can be *synchronously* perceived. On the other hand, if the two sources of sensory information are *asynchronously* perceived, the brain would segregate the two stimuli. Accordingly, multisensory integration is more likely or stronger when the constituent sensory stimuli originate from approximately the same location and at the same time.

The evolution of multiple sensory systems has enhanced the likelihood of survival for organisms living in a wide variety of environments. This is not only because the senses substitute for one another when necessary, but because they can interact, thereby providing far more information about the world than would otherwise be possible. It is thus central to adaptive behavior as it yields a better analysis by reducing the contextual noise coming from each individual sense in isolation (Ernst & Banks, 2002). For instance, when interacting with an object, its size can be judged simultaneously by both vision and touch. Compared with the noisy estimate from each individual sense separately, integrating the information from the two senses can yield a more certain estimate of the object's size depending on the environmental context. Concurrently, when two or more sensory stimuli occur at the same time and place, they are bound into a single percept, evidenced by the joint receptive fields of *bimodal neurons* located in the multisensory association areas of the cortex (Haggard, Taylor-Clarke, & Kennett, 2003).

Furthermore, as logic has it, because the output no longer resembles the response obtained to either isolated input, we can also assume that the information obtained from two or more sources has been combined to form a single novel output. Thus, perceptual experience involves not just the co-presence of multisensory features, but their coherence, or unity. Alas, the slightest asynchrony in the timing and location of two or more multisensory cues can be considerably less effective in eliciting responses than each sense alone (Stein & Meredith, 1993).

A natural extension of this was the realization that a central understanding of our perceptual systems would necessitate the involvement of how each sense is integrated with stimuli received from different sensory systems to alter each other's processing (Stein, 2012). For example, in the *McGurk effect*, what is being heard is influenced by what is being seen (e.g., when hearing /ba/ but seeing someone say /ga/ the final perception may be /da/) (McGurk & MacDonald, 1976). In this case, the /ga/ visual information and the /ba/ auditory information elicit an experience that is constitutively both audio and visual (i.e., audio-visual). Accordingly, the perceptual state that results from the processing cannot be fully decomposed into two unisensory states (i.e., audio and visual). Although this interaction involve the pairing of visual and auditory cues, it is important to note that multisensory interactions are not unique to these two senses.

Coming back to the two questions that were asked in the beginning, an essential point regarding the mechanism of the multisensory interactions is that their various manifestations are strongly dependent on the *timing* of inputs. In the example used above for instance, the *window* of synchrony between auditory and visual events is crucial, as the effect disappear when the audio-visual asynchrony exceeds approximately 300 ms (Massaro, Cohen, & Smeele, 1996; Slutsky & Recanzone, 2001). Moreover, combinations of stimuli could have very different consequences depending on their temporal and spatial relationships, and the fact that multisensory integration occurs between a set number of modalities in one direction (e.g., vision has the possibility to influence audition) (Soto-Faraco et al., 2004; Soto-Faraco, Kingstone, & Spence, 2006), does not necessarily mean that it will occur in the other direction (e.g., audition does not as easily influence vision) (Soto-Faraco & Kingstone, 2004). But how does all this relate to the topic under investigation, namely the experience of being the owner of one's body?

Some of the most important brain systems are dedicated to the maintenance of the balance between the organism and the external environment, by processing and integrating many different bodily sensory inputs (e.g., visual, auditory, tactile, vestibular, visceral, etc.), and providing an online representation of the body in the world (Jeannerod, 2006). In this view, the body representation in the brain is a complex crossroad where multisensory information is integrated in order to build the basis for bodily self-consciousness (Blanke & Metzinger, 2009).

Thus, in this essay I will address the issue of *body-ownership* from the perspective of cognitive neuroscience, paying particular attention to multisensory integration. Naturally, the body as both the subject and object of our experience creates a unique sense of intimacy, along with constituting an essential prerequisite for being able to identify oneself in the environment (Blanke, 2012; Tsakiris, 2010). When we decide to write, for example, we do not need to look for our hand in the same way that we have to look for a pen or a piece of paper, for the simple reason that it is "always there" (James, 1890). This clearly expresses a central difficulty with any experimental inquiry into the experience of body-ownership, namely designing an appropriate control condition. An ideal setting would compare conditions in which subjects have a body to one in which they do not. For obvious reasons, such prospects are visionary at best.

When searching for the appropriate explanatory levels of a phenomenon such as body-ownership in a complex biological system, it is crucial that we first successfully identify the level(s) of organization in the system at which the phenomenon of interest in actually realized. The experience of body-ownership is, to a large extent, constructed and maintained from the multisensory integration of vision, touch, and proprioception (i.e., the spatial sense of the position and movement of one's body) (Haggard, Taylor-Clarke, & Kennett, 2003). Touch and proprioception are somatic senses that stand apart from the other senses at a basic level. They are distinct senses conveyed by receptors that perfuse the body's skin and inner tissues. The mechanisms behind this appear to be distributed across distinct neural networks that vary depending on the nature of the shared information between different sensory cues. In other words, different accounts of spatial and temporal correspondence bias the system, suggesting a cascade of synergistic processes operating in a non-linear fashion at different levels of the cortex.

Various convergence zones have been identified, known as the *multisensory association areas*, where neurons receive inputs from several senses and integrate these according to various constraints. The initial cortical area to receive sensory input is the primary somatosensory cortex (S1), and here somatosensory representations follow a topographic division of body parts, also known as the *Homunculus* (Penfield & Boldrey, 1937). Although this area, or map, is a representation of our body as a whole, all sensory input from each body part are here thought of as individually distinct. The second cortical area to receive input is the second somatosensory cortex (S2), which integrates proprioceptive and tactile sensory inputs into more complex representations (e.g., size, motion, texture) (Maravita & Iriki, 2004). The third, and final, cortical area to receive input is the posterior parietal cortex (PPC), which serves as a point of convergence between vision and the lower-level somatosensory representations (i.e., S1 and S2) (Haggard et al., 2003). This area neatly enables us to determine where objects are in relation to our body, including the body as an object in itself (i.e., body-ownership) (Metzinger, 2003).

With respect to multisensory stimulation of the hand/arm, the ventral premotor cortex (vPMC) in macaque monkeys has been the most thoroughly studied area of the brain. Here, Rizzolatti and colleagues identified specific neurons that only responded to a visual stimulus when it was presented close to the monkey (i.e., within its reach in near-personal space) (Rizzolatti, Scandolara, Matelli, & Gentilucci, 1981). In other words, individual neurons that responded to touches applied to the hand would also respond to a visual object approaching the hand, but not to objects approaching other parts of the body. This suggests that the system of areas that integrate multisensory information from the body and from the space surrounding the body is a good candidate for the neural correlate of body-ownership (Haggard et al., 2003).

Recently, body-ownership has become a lively topic within cognitive neuroscience. In addition to the many clinical observations from brain-damaged patients (Blanke & Mohr, 2005), this development has been made possible by experimental methods imposing multisensory conflict as a means to induce bodily illusions in healthy subjects. These methods have provided scientists with a unique tool to start experimenting with the bodily self and to clarify the processes that produce the experience of body-ownership (Blanke & Metzinger, 2009).

A standard procedure in this regard is known as the *rubber hand illusion* (RHI) (See Figure 1), which demonstrates a bodily illusion whereby tactile sensations are referred to a synthetic hand as a result of the multisensory conflict between vision and touch (Botvinick & Cohen, 1998). In the original experiment, as well as in later versions of it (Ehrsson, Spence, & Passingham, 2004; Tsakiris & Haggard, 2005b), subjects were seated with their left hand resting on a table, hidden behind a screen. They were then asked to fixate their attention on a synthetic rubber hand in front of them. The experimenter would then use two small paintbrushes to stroke the rubber hand and the subjects' hidden hand in synchrony. After a short period (i.e., 10–30 seconds) the subjects reported having the sensation of touch in the location of the rubber hand, as if it was their own. This experience is often dramatically portrayed, with strong reactions of surprise.

A substantial amount of objective data now exists validating the RHI as a good model for body-ownership in healthy individuals. To sum up, we know that the sense of body-ownership of a hand corresponds to the perceptual integration of visual, tactile, and proprioceptive information into one multisensory object that is one's hand. This process is mediated by neural systems in key multisensory association areas that integrate visual, tactile, and proprioceptive information in temporal and spatial reference frames centered on the hand (Makin et al., 2008). To this end, the sense of body-ownership depends on a match between the look (i.e., visual) and feel (i.e., tactile and proprioceptive) aspects of the body part in question. Relevant for this observation is that the respective neural systems represent both the seen and felt position of the hand as a single percept (Graziano, Cooke, & Taylor, 2000). Put another way, the content of the changed body representation is different from, and goes beyond visual and tactile perception.

The typical experimental design in a RHI-experiment thus consists of the independent manipulation of the temporal congruency of the visual-tactile stimulation procedure, and the illusory feeling of body-ownership depends on the temporal synchrony of these two sources of sensory information. Asynchronous visual-tactile stimulation thus often involves a temporal mismatch, and it has been shown in a study which systematically varied the mismatch that a delay of 500ms significantly reduced the RHI (Shimada, Fukuda, & Hiraki, 2009). This further exposes that the RHI bear obvious similarities with the principles of multisensory integration.
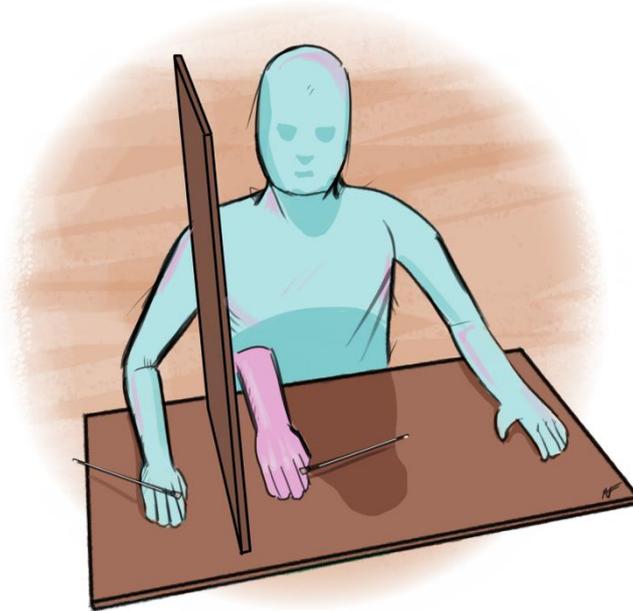
Figure 1. Canonical set-up of the RHI. The subject sees a rubber hand aligned similarly to his or her natural, unseen hand. In the *synchronous* condition, the hands are touched at the same time with identical brushstrokes at identical locations. In the *asynchronous* condition, the hands are touched at different times, eliminating the multisensory match between vision and touch and the subject's sense of ownership over the rubber hand.

As for both the temporal and spatial constraints of the illusion, it is worth emphasizing once more that it can only be evoked in the case of *synchronously* applied stimuli (Shimada et al., 2009). Similarly, the illusion is broken when the rubber hand is aligned incorrectly by spatially rotating it 90°–180° (Ehrsson et al., 2004; Tsakiris & Haggard, 2005b), or by placing it too far away from the natural hand (Armel & Ramachandran, 2003; Lloyd, 2007). Furthermore, by systematically varying the orientation of the rubber hand and the direction of the brushstrokes in order to determine its spatial compatibility, Constantini and Haggard (2007) were able to observe that the illusion is maintained as long as the hand and the brushstrokes were oriented and applied in the same direction. Given these spatial constraints, it may not come as a surprise that the illusion is severely reduced – or does not work at all – with objects that do not resemble natural hands (Tsakiris, Carpenter, James, & Fotopoulou, 2010; Tsakiris & Haggard, 2005b). What this seems to suggest is that even though we know what our own bodies are like, these temporal and spatial constraints appear in terms of what human bodies are like in general. In other words, the illusion appears constant with anything that looks like *a* hand, regardless of whether it is *one's own* hand.

The identification of such constraints provides us with important information regarding the necessary and sufficient conditions for the sense of body-ownership. Although it seems to imply that under conditions of multisensory conflict, vision typically dominates over proprioception and touch, it by no means implies that visual information is to be deemed necessary for the illusion to occur. Ehrsson, Holmes, and Passingham (2005) exposed a more sufficient criterion regarding visual information by introducing a somatic version of the RHI, in which the experimenters actively moved a blindfolded subject's left index finger so that it touched the rubber hand, while synchronously touching the subject's natural right hand. After a short period (i.e., 10 seconds) this procedure elicited the illusion that one was touching one's own hand, positively demonstrating that a visual-tactile protocol of the sense of body-ownership could be substituted by tactile-proprioceptive protocol in the absence of any visual information.

According to a controversial view held by Armel and Ramachandran (2003), they assert that the representation of our body is sufficiently plastic to incorporate new body parts, irrespective of their material composition. On their account, body-ownership is the result of bottom-up processes, and any object can be experienced as part of one's body, provided that multisensory integration is present. In this regard, the correlation of all *available* temporally and spatially congruent sensory information is deemed both necessary and sufficient for body-ownership.

However, the extent to which multisensory integration is considered a sufficient condition is a controversial issue at the heart of the neurocognitive understanding of body-ownership. In contrast to the bottom-up view, Tsakiris (2010) presents an alternative view in that body-representations involve the interpretation of multisensory integration against a pre-existing model that contains a description of the structural properties of the body. That is, sensory modalities are not simply correlated, but are integrated against a set of background conditions that preserve a coherent sense of one's body in a more top-down manner. On this latter view, multisensory integration may not be sufficient for the sense of body-ownership. For instance, if body-ownership were to be induced by synchronous multisensory stimulation as a sufficient condition, then we would expect it to be induced over objects that do not resemble body-parts. Yet, in keeping with the previously specified constraints, this expectation seems misguided.

In addition, there are physiological changes that occur while experiencing the RHI that cannot be solely accounted for by multisensory integration, without taking into consideration other higher-level representations of the body. A recent study by Moseley et al. (2008) was able to provide direct evidence of significant changes in the homeostatic regulation of the natural hand as skin temperature decreased when subjects experienced the RHI. Moreover, the degree of decrease in skin temperature was also positively correlated with the subjectively reported strength of the RHI, and could only be observed as a result of induced body-ownership, in contrast to the mere presence of synchronous visual-tactile stimulation. Thus, the sense of body-ownership of the synthetic hand has direct consequences for one's natural hand. This further acknowledges the RHI as one of the most prominent procedures for investigating the sense of body-ownership experimentally, because it allows for an external object to be treated – rather than simply recognized – as part of one's body (De Preester & Tsakiris, 2009; Tsakiris, 2010).

As such, the RHI also performs well as a model to identify the neural signatures of body-ownership. Ehrsson et al. (2004) used fMRI to scan the neural activity of subjects while they were exposed to the RHI, and found that it was associated with increased neural activity in multisensory association areas, such as the *premotor cortex* (PMC) and *posterior parietal cortex* (PPC). Tsakiris, Hesse, Boy, Haggard, and Fink (2006) further postulated the involvement of the *posterior insular cortex* (PIC). Previous studies appear consistent with the role of these areas in the sense of body-ownership, insofar as they are necessary for multisensory integration. For instance, both PMC and PPC receive extensive projections from visual and somatosensory association areas (Rizzolatti, Luppino, & Matelli, 1998). They also contain neurons that respond to visual and tactile stimulation, with visual receptive fields that correspond to the spatial coordinates of the specific body-part (Graziano, 1999). Furthermore, PIC receives afferent input from the body signaling pain, temperature, fine touch, and muscle fatigue, as well as sharing close connections with the *anterior cingulate cortex* (ACC) in mediating homeostatic emotions and bodily interoceptive sensations (Craig, 2002, 2009). Although a causal connection has yet to be established, activation in this system can sometimes be observed when "owned" body-parts are being physically threatened (Ehrsson, Wiech, Weiskopf, Dolan, & Passingham, 2007).

Such cognitive and emotional effects of the illusion are considered to be *consequences* of the causal multisensory mechanisms, and are often indicated by three primary response measurements. The first is based on questionnaires that have come to be fairly standard in the field since its first induction by Botvinick and Cohen (1998). They include two or three statements about the key perceptual effects of the illusion, such as "I felt as if the rubber hand was my hand", and five to six statements designed to control for task compliance and suggestibility.

The second is based on a more objective measure called *proprioceptive drift*, which registers the degree to which subjects experience their hand to be closer to the rubber hand that it actually is. For example, having experienced the RHI for their left hand, when asked to close their eyes and point toward their hidden left hand, subjects err in reaching, with the error being towards the location of the rubber hand (Botvinick & Cohen, 1998). Tsakiris and Haggard (2005b) also demonstrated a more sensitive version of this test where the subjects verbally report the perceived location of their hand judged against a ruler. The distance between the two locations is the proprioceptive drift, and the stronger the subjective illusion the greater this behavioral indication of the illusion. Those subjects that display the greatest proprioceptive drift tend also to be those that most strongly affirm that they own the rubber hand in questionnaires (Botvinick & Cohen, 1998). Typically, both the questionnaires and proprioceptive drift measures indicate that the illusion occurs and that subjects who experience the RHI are simply not imagining things. However, when the tactile sensation on the real hand is not synchronous with the corresponding visual stimuli on the rubber hand, then the illusion breaks down nonetheless.

The third measure is based around the idea of simulating an injury to the owned rubber hand to see if people flinch or display any emotional reactions (Armel & Ramachandran, 2003). This emotional stress response can be measured by changes in the conductance of the skin by placing two small electrodes on the index and middle fingers. Emotional responses are associated with activation of physiological responses in the autonomic nervous system, which produces increased sweating and thus increases the skin conductance response (SCR). When the finger of the rubber hand is bent backwards (Armel & Ramachandran, 2003), or a needle is stabbed into it (Ehrsson et al., 2007), the SCR is significantly augmented compared to appropriate controls.

Sensorimotor Integration

Conclusively, this communicates that body-ownership has a measurable structure, with distinct and dissociable components, and that it can be remarkably plastic and responsive to the immediate sensory context. Essentially, my body is an integral part of *me*, in a way that other objects are not. We interact with the external world through the body because the body is first and foremost an acting body. Because it is in constant motion, the relation between the body surface (i.e., the skin) and the external world are both complex and dynamic (Jeannerod, 2006).

As such, body-ownership is not influenced by our senses alone, and among its many variable components also comes the experience of being in control of one's voluntary actions. This experience that I can move and control my body is known as *agency* (Gallagher, 2000; Longo, Shüür, Kammers, Tsakiris, & Haggard, 2008). Accordingly, whereas the preceding discussion focused solely on *multisensory integration* and its role for body-ownership, the subsequent discussion will shift its focus towards the role of *sensorimotor integration* for body-ownership.

The sense or experience of agency gives a special phenomenal quality to self-generated actions and external events caused by those actions. For example, the relationship between my actions and *me* differs from the relation between observed actions carried out by other agents or without my voluntary control (Jeannerod, 2006). But are body-ownership and agency two completely different processes, or might a single process explain both these bodily experiences?

Essential for this operational distinction is that the sense of body-ownership can be present not only during voluntary actions, but also during passively generated bodily experiences. In contrast, only voluntary actions can produce a sense of agency (Tsakiris & Haggard, 2005a). The sense of agency thus involves a strong *efferent* component in the form of internally generated actions, whereas body-ownership involves a strong *afferent* component as the result of external multisensory input. This distinction is principally a methodological one, because we do not experience these components separately under normal conditions, but instead have a more general experience of our body that involves both components in a recurrent sensorimotor pattern which guides our actions and reasonably will give birth to higher cognitive functions (Tsakiris & Haggard, 2005a). As such, we sense in order to move, and move in order to sense.

Another way to get at the distinction is to envision the case of *involuntary movement* in that I experience that I am moving, and consequently that it is my movement. Hence, I have a sense of ownership for the movement and the body-part that is passively moved. At the same time, I do not have a sense of agency for such movement, since it is not I who caused it. In that regard, the sense of agency is a pre-reflective sense that I am in control of my actions (Gallagher, 2000). In this study, I will examine such wider implications on how agency can influence body-ownership.

Since it has been demonstrated that the RHI can be induced in passive subjects, agency does not seem to be a necessary condition for changes in body-ownership (Botvinick & Cohen, 1998). However, it might still offer a strong cue to body-ownership, allowing for a much more enhanced and vivid experience? To answer this question, agency must be methodologically subtracted from body-ownership, which also highlights the importance of experimental designs that are able to separate efferent and afferent information. A methodological framework is needed to compare (a) the sense of body-ownership in the absence of a sense of agency, with (b) the sense of body-ownership in the presence of a sense of agency. In order to approach this issue empirically, Tsakiris, Prabhu and Haggard (2006) sought to establish that the RHI could also be induced with voluntary and involuntary actions, thereby acting as a visual-motor substitute to the traditional touches in the more standard visual-tactile protocols (Botvinick & Cohen, 1998; Ehrsson et al., 2004; Tsakiris & Haggard, 2005b). Instead, what Tsakiris et al. (2006) showed their subjects was either a real-time (i.e., synchronous) or a delayed (i.e., asynchronous) video image of their hand while their finger moved either voluntarily or involuntarily. In the involuntary condition, the subject's finger was lifted by a string like a marionette, producing a purely sensory correlation between vision and proprioception. In the voluntary condition, the subjects moved the finger themselves, adding a motor command. Subjective reports in the involuntary condition confirmed the experience of body-ownership without the experience of agency; whereas in the voluntary condition, subjects reported clear experiences of both body-ownership and agency. These results provided added support for a division between body-ownership and agency, as well as a first step in showing how the presence of agency modulates body-ownership, which had previously been distinguished on purely conceptual grounds.

Ludwig Wittgenstein (1953/1999) notoriously asked once: "What is left over if I subtract the fact that my arm goes up from the fact that I raise my arm?" (§621). Thus, in their attempt to find an answer to his question, Tsakiris et al. (2006) examined whether the sense of agency, which is present during voluntary (i.e., body-ownership and agency), but not involuntary movement (body-ownership only), was able to promote body-ownership. A serious limitation, however, is that their study, along with many others trying to capitalize on their method (Dummer, Picot-Annand, Neal, & Moore, 2009; Yuan & Steed, 2010), were not designed to directly dissociate body-ownership and agency in a single RHI-protocol. These studies were largely based on manipulating visual feedback to either match or mismatch the participant's voluntary action. But since voluntary action always involves an inseparable combination of efferent and afferent information, their design makes it difficult to isolate experimentally the specific contributions between the two. In other words, no condition with agency without body-ownership was included, and thus agency was always present in the context of body-ownership. To that extent, the data of these previous studies may therefore confound the neural correlates of body-ownership, since it is not possible to test for double dissociations (Kalckert & Ehrsson, 2012).

The research that has been carried out in the field since then has examined body-ownership with all kinds of combinations of multisensory and sensorimotor stimulation (See Table 1). But first let us use this table to get an overview of the field up to this point. After Botvinick & Cohen (1998) had pioneered the visual-tactile protocol with the RHI, it was expanded upon with physiological (Armel & Ramachandran, 2003), as well as neurological (Ehrsson et al., 2004) measures. Soon afterwards, Ehrsson et al. (2005) introduced the somatic version (i.e., tactile-proprioceptive) of the RHI, showing that it was possible to induce body-ownership without the use of vision. Following the breakthrough of Tsakiris, Haggard, Franck, Mainy, and Sirigu (2005) who took the field from combinations of *multisensory* stimulations into the realm of *sensorimotor* stimulation with their visual-motor protocol, Tsakiris et al. (2006) tried to compare the visual-tactile (VT) and the visual-motor (VM) protocols. However, as previously stated, their design did not allow for a double dissociation to be made since they used two separate procedures. As such, they were only able to make a correlative assessment between the two.

Several studies have since tried to expand on the idea of trying to separate body-ownership and agency using the same design, as well as trying to improve the measures to solve this, but with mixed success (Dummer, Picot-Annand, Neal, & Moore, 2009; Yuan & Steed, 2010). However, following the work of Walsh, Taylor, and Gandevia (2011), a novel experimental protocol emerged in the form of a clinical three-way integration (i.e., visual-proprioceptive-motor) that was able to separate proprioceptive (i.e., efferent) from motor (i.e., afferent) information. In other words, they developed a technique that clearly could show that muscle receptors contribute to the experience of body-ownership in the absence of actual movement. By exciting the muscle receptors in the hand they were able to induce an illusion of body-ownership of a plastic finger. This still occurred when the contribution of skin and joint receptors was removed using local anaesthetics. Again, it seems that the synchrony of sensorimotor stimuli is more important to establish body-ownership than the mere presence of multisensory input.

Table 1

Chronology of Experimental Protocols

Experimental Protocol	Authors	Measures
Visual–Tactile	Botvinick & Cohen (1998)	Subjective, Behavioral
	Armel & Ramachandran (2003)	Physiological
	Ehrsson et al. (2004)	Neurological
Tactile–Proprioceptive	Ehrsson et al. (2005)	Neurological
Visual–Motor [a]	Tsakiris et al. (2005)	Subjective
Visual–Tactile vs. Visual–Motor [a]	Tsakiris et al. (2006)	Behavioral
	Dummer et al. (2009)	Subjective
	Yuan & Steed (2010)	Subjective, Physiological
Visual–Proprioceptive–Motor [b]	Walsh et al. (2011)	Subjective, Behavioral

[a] Proprioception is considered to be intrinsically linked to voluntary action, and could not be separated.

[b] These protocols include an experimental design that could dissociate proprioception from motor action.

Hypothesis

What can be inferred from previous studies is that *visual-tactile* (VT) and *visual-motor* (VM) synchronous stimulation have been shown to be important for inducing a body-ownership illusion, with each stimulus protocol (i.e., procedure) tested either separately (Botvinick & Cohen, 1998; Tsakiris et al., 2005) or correlated (Tsakiris et al., 2006; Dummer et al., 2009). As such, earlier results from comparison of the effects of VT and VM *correlations* on body-ownership illusions have been quite diverse. Nonetheless, to my knowledge, little work has been carried out on testing the *relative contributions* and possible *interactions* of VT and VM contingencies implemented in the same experimental design in order to manipulate the two stimuli protocols independently (See Figure 2). The main reason behind why this has not been done is the methodological difficulties encountered in the attempt of applying touch to body-parts in motion (i.e., active VT stimulation). Seeing as tactile information is absent in recent literature, as well as taking inspiration from the study by Walsh et al. (2011) who managed to implement a three-way integration protocol, I will try to integrate visual, tactile, and motor information as part of the same experimental protocol (i.e., visual-tactile-motor) (See Figure 3). With the use of novel immersive virtual environment technology as an experimental tool, I will optimistically be able to test a few predictions that have otherwise been difficult to pursue:

(1) The main unresolved issue pertains to what extent integration from many different combinations of sensory-motor channels is more important than certain channels being more important than others. For instance, as previous studies made *correlations* of the effects of visual-tactile with visual-motor protocols, it is predicted that an *interaction* between visual-tactile and visual-motor stimulation should induce a stronger integrative effect of body-ownership (i.e., three over two sensory-motor channels) (See Figure 3). In other words, the effect on the sense of body-ownership should be greater than would be expected from a mere additive effect of temporal congruency. In statistical terms, this effect should reveal a significant interaction effect in the factorial design (See Figure 2).

(2) However, this also means that information from many channels has to be integrated. The central issue here amounts to being able to integrate tactile sensations with motor information, and along with vision to be evaluated for congruency. Hence, there are not only more channels to channel information from, but also potentially more channels to account for when it comes to the spatial and temporal constraints of the illusion. Accordingly, in the case of an observed interaction (1), it is predicted that there might exist a trade-off between the *relative contributions* of different information channels.

Temporal Congruency of Visual-Motor Stimulation

	Synchronous	**Asynchronous**
Synchronous	$VT_{Sync} + VM_{Sync}$ (Both)	$VT_{Sync} + VM_{Async}$ (Only Tactile)
Asynchronous	$VT_{Async} + VM_{Sync}$ (Only Motor)	$VT_{Async} + VM_{Async}$ (None)

(Left vertical axis: **Temporal Congruency of Visual-Tactile Stimulation**)

Figure 2. Experimental Design. A 2 × 2 factorial design was used, with the two factors being temporal congruency of visual-tactile (synchronous, asynchronous), and visual-motor (synchronous, asynchronous) stimulation. It was a between-group with participants randomly assigned to one condition. In one group the induced illusion was measured when both touch and voluntary action were synchronous with vision. In two further groups when only one of touch or voluntary action was synchronous with vision, and a fourth group when neither was.

(1) In the case of an existing trade-off (2), and based on previous observations from
Dummer et al. (2009) and Yuan and Steed (2010) which indicates that visual-motor
integration may not be as strong as visual-tactile integration, it is further predicted that
the sense of touch will be exposed as the most effective sensory channel in mediating a
stronger effect of body-ownership, and should reveal a significant main effect in the
factorial design. Because the skin forms the boundary between the body and the external
world, touch may have a more weighted role in the experience of body-ownership. For
instance, we can use vision to see parts of our own body, but also the parts of other
bodies in external space, and so vision alone cannot account for the sense of body-
ownership to the same degree as touch. By similar means, proprioception is non-
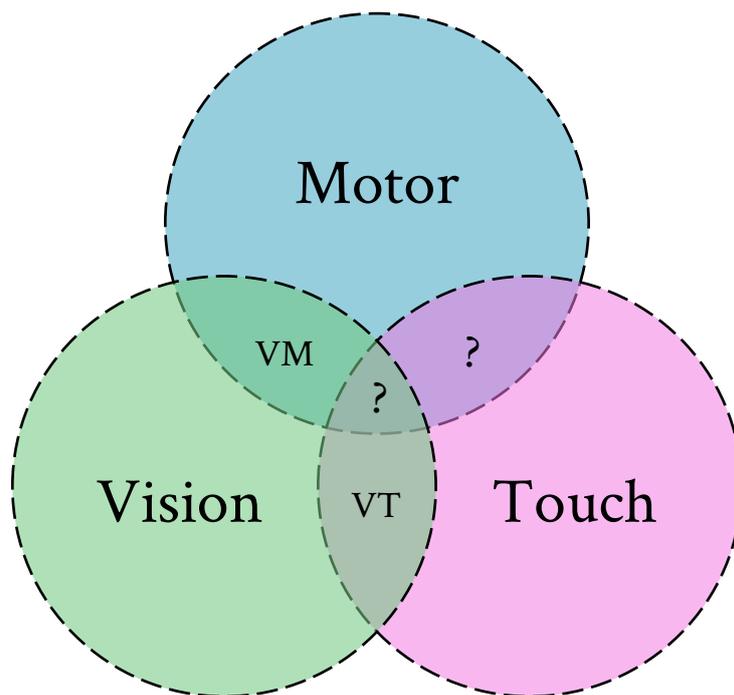conscious, whereas touch makes us consciously aware of any event occurring to the body.

Figure 3. Visual-Tactile-Motor Protocol. Visual stimuli have dominated in the field, because ambiguities
regarding visual representations of the body are both fairly convincing and are easy to produce. Visual-tactile
(VT) and visual-motor (VM) information have previously been correlated, answering for a major experimental
protocol in body-ownership research. However, the two "question marks" represents unexplored terrain in the
field, and it is hypothesized here that this visual-tactile-motor protocol could provide the missing links.

Methods

Blascovich et al. (2002) emphasize that a general assumption that seems conspicuous in all psychological research is that experimental manipulations of perceived and imagined stimuli are essentially equivalent for understanding psychological processes, at least in terms of the methods and stimuli they use (e.g., written scenarios). Although we can debate the logic behind this assumption, the pragmatic value certainly strengthens its appeal. Experimental manipulations of imagined stimuli cost less, require less effort, and provide a greater degree of experimental control (i.e., precise manipulation of independent variables). However, a greater degree of experimental control often comes at the cost of ecological validity (i.e., the extent to which an experiment is similar to situations encountered in everyday life). Consequently, a trade-off typically exists between experimental control and ecological validity. Technological advances have allowed researchers to lessen this trade-off by facilitating an increase in ecological validity without entirely sacrificing experimental control (Blascovich et al., 2002). For example, photographs and audio-recordings began to accompany the written scene early on, and the development of inexpensive video-recordings allowed subjects to experience controlled stimuli. Digital recordings and editing capabilities have also granted researchers control over the way stimuli are presented. More recently, the advent of *virtual reality* (VR) opened up for new and exciting possibilities for researchers to the prospect of eliminating the trade-off altogether.

VR, or *virtual environments* (VE), can for the purpose of this discussion be defined as a synthetic representation of a natural or imagined environment (Blascovich et al., 2002). Moreover, an *immersive virtual environment* (IVE) is one that perceptually surrounds an individual, and is primarily visual, auditory, haptic (i.e., touch), or any combination of these sensory modalities. Arguably, psychologists have been creating virtual (i.e., synthetic) environments for decades utilizing staged scenery, props, and actors. The notorious obedience environments by Milgram (1963) and Zimbardo (1973) are good examples of synthetic environments whose impact was so undeniably strong as to raise major ethical debates. However, these synthetic environments are costly and difficult to control, as well as replicate.

In accordance with the predictions based around the hypothesis, the overall aim for this study has been to take advantage of *immersive virtual environment technology* (IVET) to capitalize on its methodological value in terms of manipulating variables that are otherwise hard to control for. Hence, the focus of this study has not been to study IVET as an *object* with regard to user experience, but rather as a *method* for creating a more controlled synthetic environment that may otherwise be too expensive or impractical to achieve in a natural setting. The rationale behind this would be that it is easier to manipulate the perception of matter, than matter in and of itself.

Since we are able to completely immerse the body from the natural world, it means that the only constraint in stimuli manipulation is how we map the control condition from the natural body to the virtual one. Thus, the more we hide from the user, the more we can manipulate and control for. Starting from this observation, the question now concerns to what extent IVET is able to achieve what has been considered difficult to control for in research on body-ownership:

(1) The possibility of dissociation of stimuli that is invariably inseparable in the natural world. By *disrupting* distinct channels of information that are physiologically linked we can learn about their individual contributions to the mechanism of body-ownership.

(2) The voluntary movement of a synthetic body that is not considered to be a natural extension of one's body. By *synchronizing* distinct channels of information in real time, we can manage to create illusions that extend beyond the constraints of the RHI.

Box 1

Basic functions of IVET

A virtual reality system typically delivers stereoscopic images, generated in a graphics engine on a computer, to each of the user's eyes separately, which are then optically converged into a single image and updated in real time. A database will hold all the information that describes a particular scene in the IVE. The rendering of the scene is determined by the head position and orientation of the user, which must be tracked in real time by a motion-tracking system. The tracking system sends a continuous feed of tracking data to the computer, which is therefore able to generate the appropriate images.

Materials

A *head-mounted display* (HMD) (Oculus VR, 2012) with added support for head-tracking and motion-tracking systems was used in this study to fully render an IVE for the participants. The integrated *head-tracking* system determines the participant's position and orientation inside the IVE. That is, with regard to visual information, if the participants choose to turn their head to the right, they view what is located on their virtual right. This is intended to create a strong sense of immersion in the virtual environment by effectively creating a first-person perspective. As such, an HMD is little more than a wearable TV without a way to track the participant's head.

In order to render the representation of hand movements, since they are objects that move physically in the natural world, the set-up also demanded an external *motion-tracking* system. Traditionally, the ideal solution has been to use video-tracking, or motion-capture technology. However, the disadvantage with such large-scale systems is their inability to capture smaller muscle movements, such as fingers and facial expressions. The alternative is to use *motion-sensing* technology, which instead of manually tracking the position of the body, senses or registers it much like a burglar alarm. For this purpose, a device called Leap Motion (Leap Motion Inc., 2013) was used, which is a small USB peripheral that is designed to be placed on a physical desktop, facing upward. It senses a hemispherical area to a distance of about one meter above the surface of the desktop, and supports hand and finger motions as input, analogous to a mouse, but requiring only the natural movements of one's hands. However, in order to be able to create virtual representations of movement with sufficient reach in depth and proximity to virtual objects, the Leap Motion was mounted on the faceplate of the HMD using duct tape. This custom-built design (See Figure 5) allowed for perfect calibration of the Leap Motion, since it demanded to know where the HMD were relative to its position for it to properly register the changed perspective in the IVE. Hence, together with the integrated head-tracking of the HMD, if the participant kept his body still and only moved his or her head as if to look at the hand from a different perspective, then the hand would appear to be stationary from that point of view (i.e., visual-motor congruence between the participants' actions and the movement that they see).

Most stimuli material, including the virtual room and the hand-models, was developed and implemented using the Unity 3D game engine (Unity Technologies, 2014) by Johnathon Selstad (personal communication, 2014). Johnathon agreed to share one of his projects with me; a demo which he has created using a new software development kit (Leap Motion, Inc., 2014) that enable rigged skeletal hand tracking (See Figure 4). Added virtual objects were custom-modelled by Marcus Toftedahl and Robin Gode to fit the experimental design using the freely available Unity asset store. With all this in place, the virtual hand-model made hand and finger tracking robust to obstruction. What this means is that the participants were able to turn their hand vertically, make a fist, clap their hands, or intertwine their fingers without losing track of the hands. Hence, the stimuli material that is described here demonstrates a simple and reasonably low-priced method for providing an element of static tactile feedback from virtual objects inside the IVE. For instance, imagine that you move, and the virtual body moves in correspondence with your movements. Imagine then that you touch something in the IVE and you feel the tactile sensation. These events add significantly to the reality of what is being perceived and therefore increasing the likelihood that you would respond realistically to virtual events and situations.
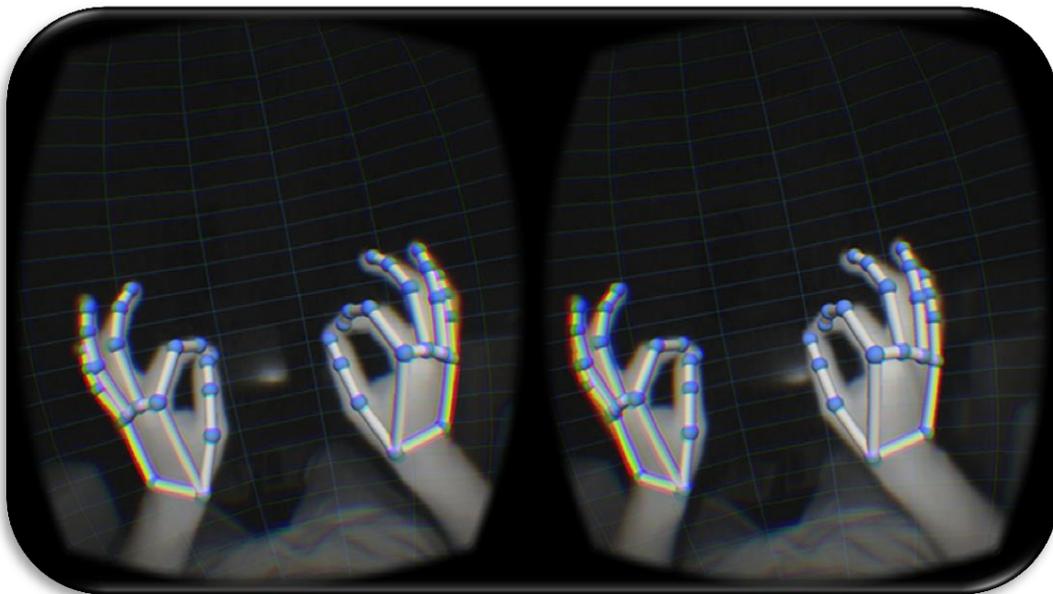

Figure 4. Rigged skeletal hand tracking. This image shows a depiction of the one-to-one correspondence between the virtual scene and reality using the overlay of rigged skeletal hand tracking on a pinch gesture.

Measures

A majority of previous studies in the field has used subjective reports as a measure of the strength of the illusion. However, by the very nature of IVET, there seems to be indications that subjective report measures (i.e., questionnaires) will never be sufficient as a measurement tool. Aside from the usual demand characteristics, one reason is that they are not able to avoid methodological circularity in the sense that the very asking of questions may bring into being – post-hoc – the phenomenon that the subjective report is supposed to be measuring. Slater (2004) demonstrated that while it is possible to achieve high reliability from subjective reports, these measures can actually be the manifestation of the wrong latent construct. In other words, when subjects are faced with a dilemma due to the abstract nature of the questions and the novelty of the situations in which the questions are raised, they simply map the questions onto some other underlying construct that is more reasonable to them. Moreover, under normal conditions, we are continually aware of our body, rather than it being a quality that varies over time. Thus, the subjective measure of body-ownership requires a graded score of a sensation that is typically invariant. Consequently, when dealing with abstract experiences, the best way can sometimes be not to listen to what subjects say in response to direct inquiries, but instead focus on more statistically reliable differences and indirect behaviors to see if it coincides with our expectations.

As already discussed, one such measure that has proven notoriously popular within the field is *proprioceptive drift*. It is widely considered a quantifiable behavioral correlate for the sense of body-ownership as it measures to what degree subjects experience their natural hand to be closer to the synthetic hand than it actually is. For instance, after having experienced the RHI, when subjects are asked to close their eyes and point toward their natural hidden hand, they make a reaching error toward the location of the rubber hand (Botvinick & Cohen, 1998). As drift arises as a consequence of the illusion, it can thus be used as an indirect measure of the illusion. Yet, the usual measure for proprioceptive drift has not been performed in this study. Partly because there should be no drift since the virtual hand and the natural hand are actually in the same place. Alas, even if drift would occur, it can be difficult to dissociate from delay in the tracker.

In general, the more conventional subjective (i.e., questionnaires) and behavioral (i.e., proprioceptive drift) measures employed in body-ownership research are *offline* measures in the sense that they require conscious post-judgment of the task. However, since the effects if any, of this experiment are going to be subtle, I instead set out with the intention to obtain physiological *online* data for this effect. I arrived at measuring participants' evoked *skin conductance response* (SCR), which is a measure used to record the electrical conductance of the skin, indicative of autonomic arousal and stress. Consequently, this will lead to increased heart rate (HR) and blood pressure, which prompted me to complement the SCR data with *electrocardiography* (ECG).

In essence, the idea here was to introduce a threatening event to the participants' virtual hand in order to elicit an emotional stress response, which is associated with activation of physiological responses in the autonomic nervous system. This produces increased sweating and in turn increases the SCR. Based on previous studies, the degree of autonomic arousal experienced when the rubber hand is being threatened is directly correlated with the strength of the illusion (Armel & Ramachandran, 2003), as well as causing similar levels of activity in the brain areas associated with arousal as when the subjects natural hand is threatened (Ehrsson et al., 2007). Moreover, in line with the hypothesis, the purpose was also to explore whether or not the SCR and HR were affected under the different experimental conditions compared to the appropriate controls. If the predictions were to be accurate, it would be expected of those participants experiencing a higher degree of body-ownership to have a greater sense of threat to their body, and for this to be reflected by an increase in the SCR, and possibly also in HR.

The SCR and ECG data was recorded with a portable NeXus-4 system (Mind Media, 2014a). Two skin conductance electrodes were attached to the pulps of the index and middle fingers, with two reference electrodes applied to the upper arm. Three ECG-electrodes were attached to the collar bones and the lowest left rib. A conductive paste was applied to all the electrodes in order to improve the signal-to-noise ratio, and the data were stored and analyzed on a second laptop computer with the Biotrace+ software (Mind Media, 2014b) supplied with the NeXus-4. The participants wore the electrodes for a couple of minutes before initiating the recordings.

Design

The design was a 2 × 2 factorial, with the two factors of temporal congruence of VT (asynchronous, synchronous) and VM (asynchronous, synchronous) stimulation. It was a between-group design with 20 participants assigned to each condition in a pseudo-randomized order (See Table 2). The rationale behind this was that participants otherwise adapt quite fast to these kind of disruptions, and learn to operate in the new conditions more efficiently.

Table 2

The Experimental Conditions

Condition	N	$M_{age} \pm$ SD
(1) Visual–Tactile (synchronous) + Visual–Motor (synchronous)	20	28 ± 5
(2) Visual–Tactile (synchronous) + Visual–Motor (asynchronous)	20	27 ± 7
(3) Visual–Tactile (asynchronous) + Visual–Motor (synchronous)	20	29 ± 5
(4) Visual–Tactile (asynchronous) + Visual–Motor (asynchronous)	20	28 ± 9

Participants

Volunteers were pre-screened in order to gauge whether they were capable of experiencing the RHI. This was necessary because approximately 20% of the population seems to be "immune" to its induction, without any conclusive evidence as to why (Ehrsson et al., 2004; Lloyd, 2007). 87 volunteers in total were recruited for the study, while 7 volunteers were excluded due to technical failures or misconceptions of the procedure. The remaining 80 (M_{age}=28 ± 8) volunteers that participated in the study were each given written informed consent, briefing them of the potential risks involved with IVET (i.e., motion sickness), and advised that they could withdraw from the experiment at any time if they so desired. None of the participants had any previous experience with the task and were unaware of the experimental hypothesis.

Procedure

The participants were seated with their hands resting prone on a table, which could be adjustable in height, and were equipped with the SCR and ECG sensors. They were fitted with the custom-made HMD that showed them the virtual projection of two hands, which was displayed as resting on a virtual table (See Figure 5). Once the participants had entered the IVE, they were instructed to look around and try out various hand movements for purposes of acclimatization to the equipment and become familiar with the scene. They were then asked to observe for thirty seconds before being asked to place their hands back on the table in front of them. The set-up was now calibrated by adjusting the height of the table in order to correspond to the height of the virtual table, such that the participants' felt the surface of the table at the same time as they saw the virtual hand touch the virtual table. Because the participants wore the SCR sensor on their non-dominant hand, they were at this point instructed not to move it during the rest of the experiment in order to reduce any artifacts from movement in the SCR.
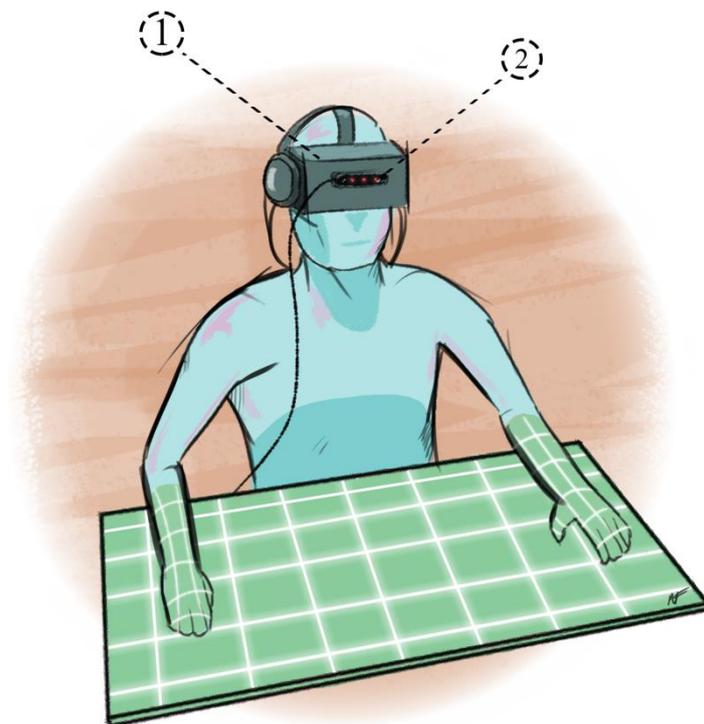

Figure 5. Experimental Procedure. (1) HMD (Oculus Rift); (2) Motion-sensor (Leap Motion). The participant is seated with his hands resting prone on a table, which could be adjustable in height to match the virtual table.

Following the training period, all participants completed one block with four 90 second trials (i.e., 6 minutes), with each block consisting of alternating sets of VT and VM stimulations represented by each of the experimental conditions (See Table 2). Four trials were used to optimize the statistical variance, and correct for any unknown variables during the procedure. A timer was implemented in order to play a sound to signal to the participant through the headphones the end of each trial, and the start of the next one. Between each trial, there was a rest period of 30 seconds to allow for the SCR/HR to normalize before the next trial began. This was of particular importance, since during this time, instead of obtaining a standard baseline measure before the start of the whole experiment, it was conveniently obtained during each rest period after the SCR/HR had normalized, as a means of producing more reliable results.

In the first condition (1), the participants were instructed to tap their fingers repetitively against the table surface, thereby providing active tactile feedback (i.e., visual-tactile-motor). They were encouraged to alternate in a non-rhythmic pattern, so that the actions were made effortful. In the control condition (4), the temporal congruence of the visual-motor information was manipulated by introducing a perceptual delay in the rendering of the movement (i.e., 500ms), thus creating a conflict between the voluntary action (i.e., motor) and the observed movement (i.e., vision). By doing this, a conflict was at the same time created between the touch (i.e., tactile) and the observed touch (i.e., vision). In the third condition (3), the temporal congruence of the visual-tactile information was manipulated by introducing an invisible break in the contact surface of the virtual table, such that the participants felt the natural table but saw that the virtual hand was not actually touching the virtual table at the same time. Hence, although the movement of the virtual hand corresponded to the participant's movements, there was a conflict between the touch (i.e., tactile) and the observed touch (i.e., vision). In the second condition (2), a standard protocol for involuntary movement was used (Tsakiris et al., 2006; See page 18), though modified to fit this particular experimental set-up. Instead of using strings, all fingers of the participant's hand were strapped to the corresponding fingers of the experimenter's hand using Velcro-straps, acting like a marionette to create a conflict between the felt movement (i.e., motor/proprioception) and the observed movement (i.e., vision).

At some time during the last trail of the induction period, there was an event that was programmed to act as a threat to the participant's "owned" virtual hand. This consisted of the sudden appearance of a virtual knife above the designated virtual hand using a Unity script for tracking the coordinates of its relative position to ensure that it always fell on the hand that was carrying out the task (See Figure 6). Each time the virtual knife fell on the virtual hand it took approximately 2 seconds from the time that it entered the participant's field of view. The motion was performed so that it was always ending right before (i.e., 1 cm) the point of contact with the virtual hand, so as to motivate a defensive response rather than the experimenter being forced to synchronize tactile feedback from the virtual knife to preserve the immersive effect, as well as not to compromise the design since not all conditions include touch as a source of information.
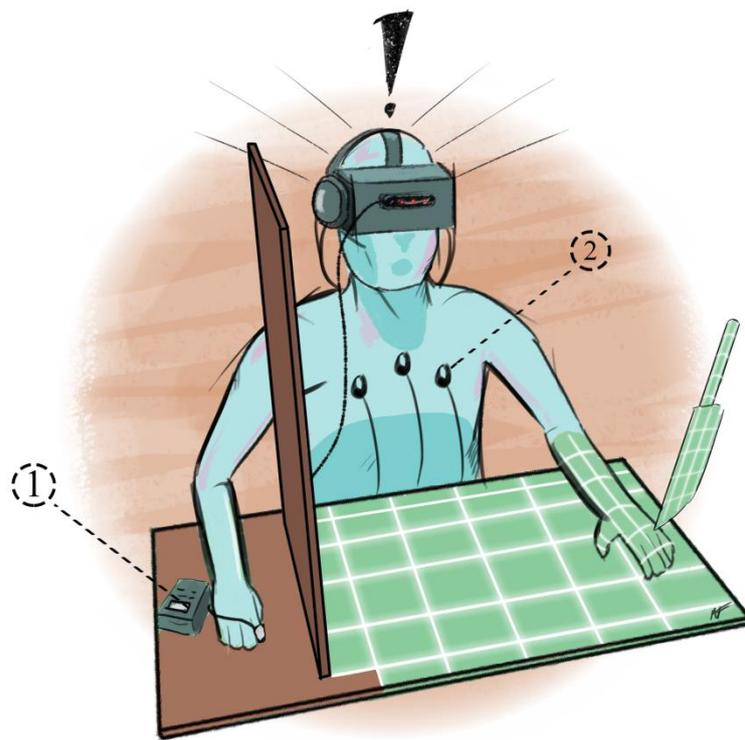

Figure 6. Threatening Event. (1) SCR (NeXus-4); (2) ECG (Ag-AgCl electrodes). Each participant was at some time during the last trail of the induction period introduced to a virtual threat (i.e., knife) to their "owned" virtual hand, intended to elicit a stress response. It was expected that those experiencing a higher degree of body-ownership to have a greater sense of threat to their body, reflected in greater physiological responses. In this illustration, the partition displays the division between the experienced scene and the occluded natural one.

Results

The period of interest for the physiological measures is immediately after the threatening event. However, the physiological responses typically do not occur immediately after stimulus onset since the threatening event evokes a chemical reaction in addition to the electrical, which usually is a slower response. The SCR signal was collected at a sample rate of 30 Hz (i.e., 30 ms intervals), and smoothed (i.e., baseline-corrected) with a median filter over 10 time-intervals corresponding to a window of 500ms each (See Figure 8-9). The SCR was identified as the peak that occurs up to 10 seconds after stimulus onset (i.e., from when the virtual knife first entered the participant's field of view). The amplitude of the SCR was identified as the difference between the maximum and minimum value, measured in microsiemens (μS). HR was also determined from the consecutive peak intervals of the ECG, while the software calculated the interbeat intervals, measured as a change in beats per minute (b.p.m). The data were cleaned of artifacts by excluding all minimum and maximum values three SD's from the mean, as such outliers are unlikely to reflect valid responses from these measures (Ehrsson et al., 2007).

In Table 3, the means ± SD for each measure are displayed. In general participants seem to elicit stronger physiological reactions on both measures to the threatening event in the synchronous visual-tactile-motor protocol (1) compared to (2), (3), and (4) in a linear fashion. This could be considered an early indication of the data supporting parts of the hypothesis.

Table 3

Means ± SD for SCR and HR for all Experimental Conditions

Condition	SCR (μS)	HR (b.p.m)
(1) Visual–Tactile (synchronous) + Visual–Motor (synchronous)	0.94 ± 0.21	74 ± 10
(2) Visual–Tactile (synchronous) + Visual–Motor (asynchronous)	0.38 ± 0.17	71 ± 9
(3) Visual–Tactile (asynchronous) + Visual–Motor (synchronous)	0.62 ± 0.19	73 ± 11
(4) Visual–Tactile (asynchronous) + Visual–Motor (asynchronous)	0.22 ± 0.07	70 ± 8

Note. Means ± SD are calculated for each condition for the period 0-10 seconds from the threatening event.

A two-way factorial ANOVA was used to test for statistical differences between the two independent variables across all four conditions. A significant main effect for the temporal congruence of visual-tactile stimulation on SCR could be observed, $F_{1,76} = 7.25$, $p=0.01$. This shows that participants who received *synchronous* visual-tactile stimulation evoked stronger physiological responses than participants who received *asynchronous* visual-tactile stimulation, regardless of whether they received any visual-motor stimulation. A significant main effect for the temporal congruence of visual-motor stimulation could also be observed $F_{1,76} = 16.2$, $p=0.005$, which similarly shows that participants who received *synchronous* visual-motor stimulation evoked stronger physiological responses than participants who received *asynchronous* visual-motor stimulation, regardless of whether they received any visual-tactile stimulation. In addition, a significant interaction effect could also be observed $F_{1,76} = 5.8$, $p=0.03$. This demonstrates that the magnitude of the effect between participants who received either synchronous or asynchronous *visual-motor* stimulation evoked stronger physiological responses when also receiving synchronous, compared to asynchronous, *visual-tactile* stimulation.
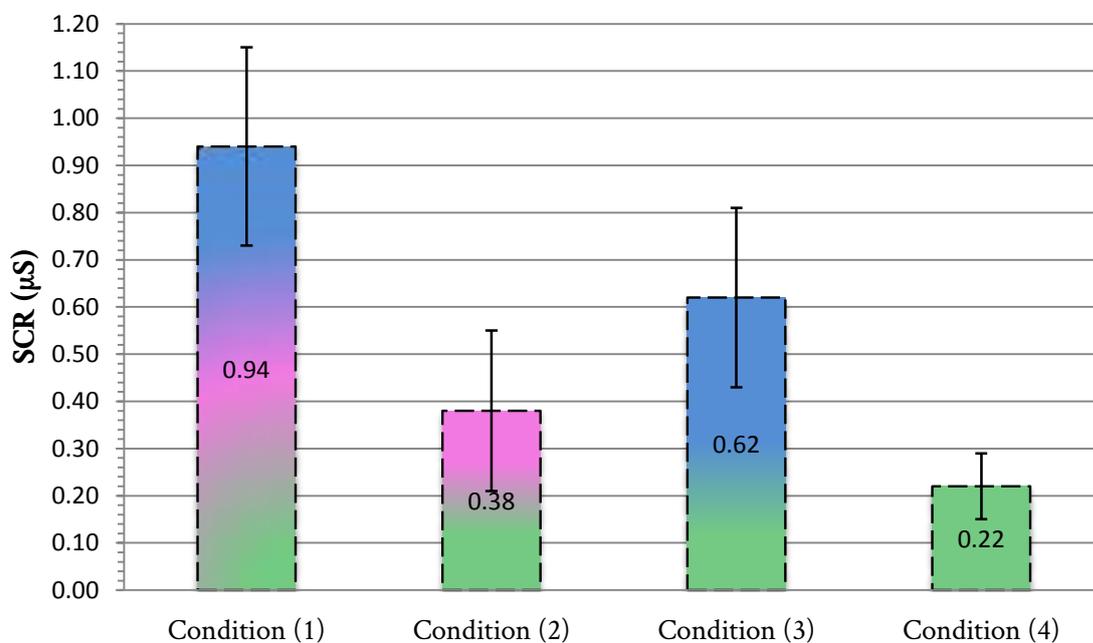

Figure 7. Means ± SD for SCR for each condition for the period 0-10 seconds from the threatening event. Color codes for Vision (Green), Touch (Pink), and Motor (Blue), measured in microsiemens (µS).

Moreover, the skin conductance amplitude and the change in HR from baseline to the threatening event are positively correlated, $r= 0.43$, $p=0.01$. In Figure 8 and 9 below are two mean samples for the period 0-5 seconds from the threatening event. This provides an evaluation of the descriptive differences from the critical event of stimulus onset, which has not been accounted for in the inferential statistics. This is elaborated upon more in the discussion.
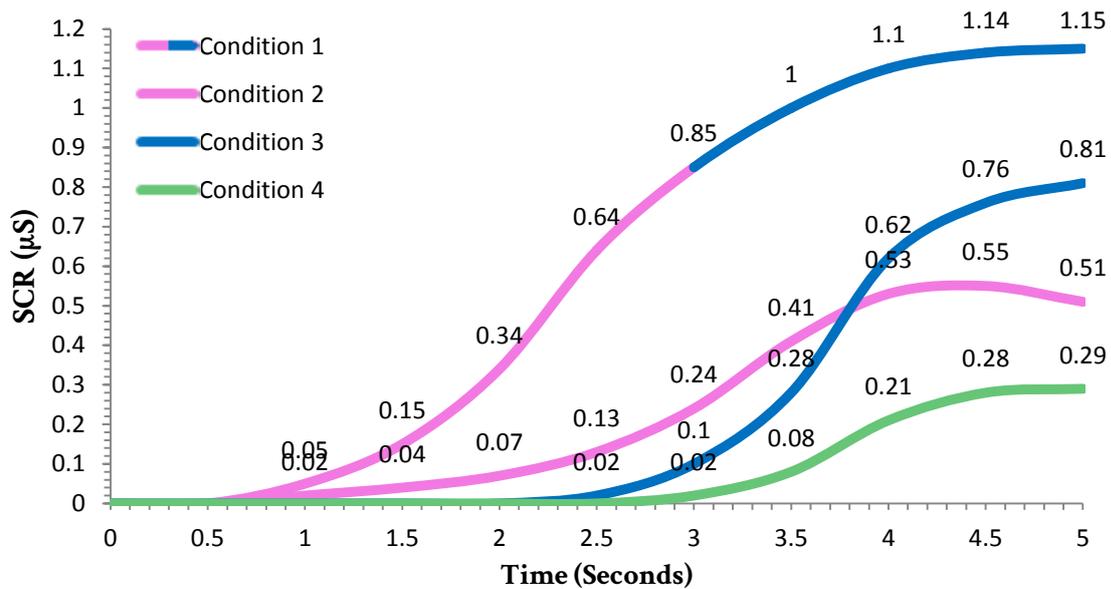

Figure 8. Mean relative SCR responses for each condition for the period 0-5 seconds from the threatening event.
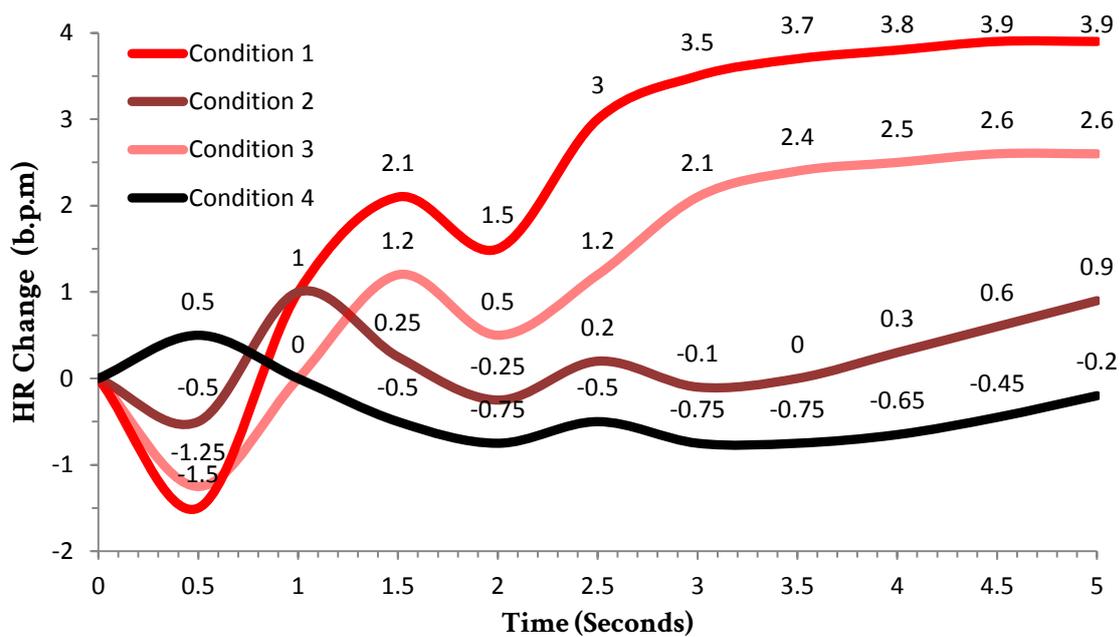

Figure 9. Mean relative changes in HR for each condition for the period 0-5 seconds from the threatening event.

Discussion

In keeping with the predictions outlined in the hypothesis, the observed significant interaction effect clearly supports the first prediction in that the integration between vision, touch, and motor stimulation elicits a stronger integrative effect on body-ownership when presented together *online* under the same experimental protocol. On that account, since the interaction rejects a purely additive effect, it also exposes the second prediction to be fairly accurate in that there is a trade-off between the relative contributions of tactile and motor information. Alas, the two main effects of the experiment deviate from the third prediction of the hypothesis in that motor, rather than tactile, information seem to be a more effective sensory-motor channel in mediating body-ownership. The third prediction was predicated on the assumption that the observations from Dummer et al. (2009) and Yuan and Steed (2010) were correct. However, seeing as both these studies formed their conclusions mostly based on subjective reports, this might potentially serve as an example of the problem with using subjective measures in body-ownership research, since they may be heavily biased towards tactile information. For instance, the third prediction was made resting on the fact that touch seem ideal in terms of recruiting more attentional resources due to its conscious nature, compared to the non-conscious nature of proprioception. Consequently, participants who are asked to report their experiences are going to have a difficult time reporting experiences that are non-conscious.

Yet, as we aim to take a closer look at the onset time for the threatening event (See Figure 8), we can see a slight indication that condition (2) which involves synchronous visual-tactile stimulation gives off a much faster response (1 second), although weaker in amplitude, compared to condition (3), involving synchronous visual-motor stimulation (2.5 seconds). This seems to suggest that tactile stimulation (i.e., afferent) in some sense is more sensitive than motor stimulation (i.e., efferent) in the initial stages of the response, but as soon as the brain catches up with the seemingly more complex process of the motor command, the response gains in amplitude. Besides, as we can see in the first condition (1), the interaction of these two responses seems to get a combined effect of a fast high-amplitude response, as is also reflected in Figure 9.

Although much of the design of the experiment could rule out potentially confounding variables such as surprise, general arousal, and emotional salience of the stimuli, one major confounder that comes with the experimental equipment is of course that there is no way to tell at this point to what extent the immersive aspects of the VE influences the measured data. This is a general problem in psychological research that I discussed earlier, but one that progresses for the better as one is creating more believable synthetic environments that are able to replicate the natural environment. Ecological validity, no matter to what extent, is just the price we have to pay in order to achieve a greater degree of experimental control. However, the trade-off between ecological validity and experimental control in the case of IVET comes with good value in my opinion, and that value is only going to increase as technological advances continue to break new ground. For example, even the original RHI in some sense relies on the assumption that the same mechanisms that mediate illusory sensations conforms to the actual natural sensations.

Another confounder that we inherit with this experimental protocol, although much more serious and approachable, is the fact that it seems like motor information in general, and agency in particular, contributes something additional to the sense of body-ownership at the functional level. By functional I refer to the top-down processing of higher-order action representations. To this end, voluntary actions can be interpreted at the level of goals rather than at the level of movement (Gallese, 2000). Another example of this includes the concept of intention. The normal experience of voluntary action includes an implicit sense that the goal-directed action occurred *because* the agent had to perform it. This hierarchical structure of agency over body-ownership creates problems in terms of sensory attunement, in which voluntary actions can suppress incoming sensory information (Blakemore et al., 1998, 2000). The way this works is that the motor system predicts the sensory consequences of the action and compares it to the sensory input that is actually perceived. This way, there is no longer an incentive to receive the sensations as intensely, and so the brain attenuates the relevant information. For instance, this might explain why you find it much harder to tickle yourself; compared to if the touch was externally generated (Blakemore, Frith, & Wolpert, 1999). This may be problematic for this experimental protocol, since touch is applied through action (i.e., active tactile stimulation).

A central concern that also needs to be addressed is the experimental design, analysis, and interpretational limitations of the study. Although multisensory or sensorimotor integration can be a useful approach for research on body-ownership, it demands some deeper inspection. What, for instance, does it mean to be integrated? Are sensory input simply *combined* in an additive manner, or are they *integrated* at some localized area in the brain? Conceivably, the problem may arise because we tend to arbitrarily stipulate what it means for something to be "localized".

Consider again the hierarchical cortical structure when it comes to the somatosensory cortex discussed in the introduction. Each sensory input here is processed at different levels of organization. Hence, it seems remote to assess that the brain just combines and averages out the converging sensory inputs, as it requires more complex representations. However, I think one should be careful here, because this way of seeing things betrays a limited perspective in terms of not recognizing the fact that both low-level sensory input and high-level body representations can be seen as being on the same continuum of neural complexity, although on separate ends of the spectrum. Thus, if we want to investigate a multisensory phenomenon (i.e., body-ownership), I believe we have to recognize that its contribution stems from an integrative process, not just by being part of the previous neural organization, but of each level being functionally dependent on each other in a dynamically non-linear fashion. However, this also highlights an important issue to consider when combining the two perspectives in question.

On these terms, a brain area is implicated in multisensory integration if it responds to two or more sensory inputs presented in isolation (e.g., visual-tactile neurons to visual input and tactile input). This is well motivated by neurophysiological findings that unimodal cortical areas are separated from one another by transitional multisensory zones (Wallace, Ramachandran, & Stein, 2004), and by the proposed sensory organization of higher-order association areas (Beauchamp, Argall, Bodurka, Duyn, & Martin, 2004). On a purely additive or combined account, we are not in a position to draw any strong conclusions concerning the integration of bimodal neurons (i.e., those that respond to multiple modalities) in the multisensory association areas. In other words, neurons in multisensory association areas in the case of body-ownership may be responsive to multiple modalities, but not all of them necessarily integrate this

information such that their response to one modality is measurably altered by the presence of a stimulus from a different modality (i.e., true multisensory integration) (Calvert & Thesen, 2004). However, the way that this issue is often overlooked in the field of body-ownership research may reflect some inattention or miscommunication as to how the different modalities are presented within the neighbouring field of multisensory integration. Thus, this final part will take a critical stance regarding the implementation of the experimental design, and ultimately on how the results are analysed and interpreted with respect to these different perspectives.

What can be inferred from the previous assessment is that an additive analysis cannot account for multisensory experiences (i.e., body-ownership). A possible improvement of the methodology may then be to contrast activation obtained during unimodal stimulation (e.g., vision *or* tactile stimulation) against that produced during bimodal or multisensory stimulation (e.g., visual-tactile stimulation), and attempt to identify greater responses during multisensory integration than either modality in isolation (e.g., VT > V + T) (Calvert et al., 1999). Nevertheless, because additive analyses have been widely used in multisensory research, the distinction between an *additive* and *integrative* account has not yet been clearly drawn in the body-ownership research, as it seems to be based on a more liberal view of perceptual research.

The idea behind this study thus takes the liberty in terms of the assumptions made in the field of body-ownership and tries to expose participants to two stimulation procedures and to compute the interaction between them. In this way, a two-way ANOVA informs us whether the effect of one of the independent variables (i.e., temporal congruency of visual-tactile stimulation) on the dependent variable (i.e., degree of body-ownership) is the same for all values of the other independent variable (i.e., temporal congruency of visual-motor stimulation). For example, is the effect of touch on the sense of body-ownership influenced by voluntary actions and movement, and vice versa? This particular design may benefit from the involvement of bimodal or multisensory neurons that can evoke emergent processes (i.e., body-ownership) on a behavioural level not similarly recruited during unimodal stimulation on a physiological level. Thus, at the behavioural level, the design may provide a more robust method for identifying integration responses in which both visual-tactile and visual-motor conditions are present.

Interaction effects are commonly used to identify changes that occur when two factors are synchronously altered that would not be predicted from the results of altering each factor in isolation. In the context of multisensory integration, the use of interaction effects thus permits a clear demonstration that bimodal or multisensory responses cannot simply be predicted from the sum of the unimodal responses. In other words, this design, given its unsophisticated approach, also has its advantages. First, it provides a demonstration that some form of interaction has occurred as the output is significantly different from the sum of the inputs. Secondly, it shows that the conditions will necessarily ensure that the protocol meets the criteria for integration, such that temporally congruent senses are bound into a single percept (Calvert, 2001).

An alternative explanation may be that on both the behavioural and physiological level, responses might differ substantially depending on whether the participants give different attentional weight to different senses. For example, we may think of vision as the key sense in terms of binding since we primarily use vision to identify if a stimulus is synchronously applied or not. From this point of view, we could redesign the experiment in such a way that we vary the availability of visual information related to both tactile and motor information. However, important to remember is that the mechanism of multisensory and sensorimotor *interactions* is that their various manifestations are strongly dependent on the *timing* of inputs, and not so much on the mere presence of a particular sensory modality. The integration of multisensory and sensorimotor cues involves statistical inferences because each sensory modality is not equally reliable, but can vary depending on the context and the nature of the stimuli being perceived. The weight of one modality over others often depend on what modality produces the most accurate information for the action carried out, and vision tends to be the most dominant sense. This has often been explained in terms of people's attentional resources being biased toward the visual modality due to its high practical usage (Koppen & Spence, 2007). On the other hand, audition is usually more reliable than vision for localizing objects in a dark setting. Thus, for such a complex system as the brain, the optimal performance would be to assign greater weights to the most reliable sense (i.e., vision) and then adjust depending on the context. In such a way, artificial conflicts that we create are resolved in favour of the most appropriate modality.

The results of the original RHI gives us the indication that the brain is not confused as to whether a body part is real or artificial, since it is not necessary for vision alone to identify such discrepancies. Instead, vision is only one piece of the puzzle in interpreting whether or not the object in front of you should be part of you or the external world depending on the information that is being received. In the light of this study then, it is not possible to stimulate vision independently in order to convince the brain as to whether a virtual hand *should* be part of you. Similarly, it is not possible to independently manipulate a motor command without vision, because the brain will only resort to use a much more appropriate sense in determining the position of the limb (i.e., proprioception) and will most likely come to a different conclusion. Instead, what is needed is manipulation procedures that can trick the brain into making tough decisions based on whatever information is available, which emphasizes the importance of creating stimulation protocols that are able to integrate different sensorimotor combinations.

Conclusion

On the basis of these observations, this study can be interpreted in relation to previous studies to constitute just one additional sensory combination (i.e., visual-tactile-motor) to be included into the sensorimotor protocols for body-ownership, although granting it is one that has previously been difficult to investigate. The effect of IVET on physiological measures also allows for a wider objective evaluation, which hints at the prospect of using IVET to aid in our understanding of self-consciousness (Blanke, 2012). The strength of tackling the issue of body-ownership from a sensorimotor perspective is that it provides a parsimonious explanation that does not require the inclusion of higher cognitive functions, which are often hard to define and even harder to relate to neural mechanisms. The perceptual distinction between one's own body and the external world may create a necessary foundation for higher cognitive functions related to self-consciousness to emerge. Alas, here we also encounter one of the deepest theoretical problems in neuroscience; the fact that we have no idea what the correct level of analysis is. Searle (1997) has even remarked on it being "the dirty secret of contemporary neuroscience".

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